

Benthic Algae of Lake Erie (1865-2006): A Review of Assemblage Composition, Ecology, and Causes and Consequences of Changing Abundance

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ABSTRACT. Peer-reviewed literature and published reports were used to summarize knowledge of benthic algal assemblage composition and ecology in Lake Erie, and causes and consequences of temporal variation in algal abundance. Macroalgal assemblages in rocky littoral and soft substrate habitats have been reasonably well described and studied, as has the epiphyte/metaphyte assemblage associated with rocky littoral macroalgae. In contrast, little information exists for non-epiphytic microalgae in littoral habitat. During the period when algal records were reported (1865-2006), the rocky littoral macroalgal assemblage was often dominated by the chlorophyte genera *Cladophora* and *Ulothrix* and the rhodophyte *Bangia*, whereas the charophytes *Chara* and *Nitella* were most abundant in littoral soft substrate. In addition to substrate effects, assemblage composition varied as a function of depth, temperature, light levels, and nutrient concentrations. Under certain conditions, macroalgal taxa appeared to outcompete and exclude other taxa from littoral habitat. However, these organisms have also facilitated increased algal diversity by supporting epiphytes/metaphytes. In Lake Erie, significant temporal change in benthic algal abundance has been associated with: 1) eutrophication (prior to 1972), 2) oligotrophication following the Great Lakes Water Quality Agreement (1972-1985), and 3) invasion by *Dreissena* mussels (1986-2006). Increasingly eutrophic conditions were reflected by high abundance and frequent shoreline fouling by *Cladophora*, declining charophyte (such as *Chara*, *Nitella*) abundance, and invasion of rocky littoral habitat by euryhaline *Bangia*. Subsequent indicators of oligotrophication included declining *Cladophora* abundance, and increased diatom abundance in deepwater habitat. Effects of filter-feeding *Dreissena* (such as increased water clarity, phosphorus excretion) were likely causes for *Cladophora* resurgence in the 1990s, and likely contributed to return of *Chara* and *Nitella* to formerly occupied habitat. Algal assemblages clearly reflect environmental conditions in aquatic ecosystems. To accurately assess present and future conditions in Lake Erie, continued study of all benthic assemblages is recommended, with greater attention directed toward microalgae in littoral habitat than has occurred in the past.

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INTRODUCTION

Algae are aquatic, photoautotrophic, nonvascular plantlike organisms possessing chlorophyll *a* and unicellular reproductive structures (Stevenson 1996, Sheath and Wehr 2003). A variety of prokaryotic and eukaryotic, and unicellular and colonial organisms are included in this group, with taxonomic divisions distinguished on the basis of photosynthetic pigments, energy-storage products, and cell coverings (Sheath and Wehr 2003). Benthic algae, defined as algae living on or associated with submerged substrates, are critical functional components of freshwater ecosystems (Lowe 1996, Stevenson 1996). As primary producers and invertebrate food, these organisms regulate secondary production and nutrient- and energy-flow pathways in benthic food webs (Lowe 1996, Stevenson 1996). Benthic macroalgae also provide habitat for many organisms, including invertebrates, fishes, and other algae and microorganisms (Lowe 1996, Stevenson 1996). Additionally, taxonomic composition of algal assemblages is a reliable indicator of water and habitat quality (Lowe and Pan 1996, Stevenson and Smol 2003).

Lake Erie is the shallowest, southernmost, and most productive of the North American Great Lakes, and its extensive littoral (i.e., shallow) habitat, relatively warm water, and abundant nutrients are favorable to benthic algae (Bolsenga and Herdendorf 1993, Lowe 1996). Previous studies demonstrated that benthic algae are key determinants of energy and nutrient flow pathways and biotic community structure in Lake Erie, and that their abundance affects and reflects environmental conditions in the lake (Knapp and Petrie 1999, Carrick and others 2005, Higgins and others 2008). In

fact, of all Lake Erie biota, the benthic alga *Cladophora* has arguably been the most visible and influential biological indicator of water and habitat quality changes occurring since Europeans colonized the watershed (Shear and Konasewich 1975, McGucken 2000, Higgins and others 2008).

Knowledge of benthic algal assemblage composition, abundance, and ecology is requisite to understanding environmental conditions in Lake Erie. However, the extent of knowledge on Lake Erie's benthic algae isn't readily apparent because existing information is scattered across a large time period and quantity of literature. In this paper, published information from benthic algal investigations in Lake Erie is used to 1) report records of benthic algal taxa from Lake Erie, 2) summarize knowledge of benthic algal ecology and assemblage structure, and 3) describe causes and consequences of temporal change in benthic algal abundance. The information base produced from this review is intended to assist in designing future algal-based investigations in Lake Erie, and in relating results of these studies to spatial and temporal variation in environmental conditions. An additional objective was to identify understudied benthic algal assemblages, and therefore facilitate investigations that fill knowledge gaps and improve understanding of Lake Erie ecology.

METHODS

A comprehensive survey of primary, peer-reviewed literature was attempted by obtaining any journal article thought to contain information on Lake Erie benthic algae. Information from accessible books and published reports that never appeared in a peer-reviewed journal was also included. In total, 838 publications were obtained, and records and accompanying ecological information are presented from all 87 references that contained original records of benthic algal genera or species from Lake Erie (Table 1). Necessary criteria for records to be included in this review included evidence that

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organisms were alive at time of sampling, and obtained from a benthic habitat of Lake Erie proper (i.e., open lake, bay or harbor, moist substrate above the water line). Due to the historically unstable nature of species-level taxonomy for algae, and lack of extensive ecological information for most species in Lake Erie, discussion of assemblage composition, ecology, and abundance is focused at the generic level of taxonomic resolution. This is the first comprehensive review of published records and information on benthic algae of Lake Erie. Previous reviews of algae that inhabit Lake Erie benthic habitat focused on specific taxa and were conducted across multiple ecosystems (Wolfe and Sweeney 1982, Sheath 1987, Higgins and others 2008).

The Lake Erie Ecosystem

Lake Erie lies between 41° 21' N and 42° 50' N latitude and 78° 50' W to 83° 30' W longitude, and covers 25,734 km² with maximum breadth and length of 92 km and 388 km (Bolsenga and Herdendorf 1993, Haltuch and others 2000). Mean and maximum depths are 19 and 64 m, and the lake holds 484 km³ of water (Bolsenga and Herdendorf 1993). The long axis of Lake Erie parallels prevailing wind direction, causing high waves (up to 3.6 m) and fluctuating water levels in response to storms (Bolsenga and Herdendorf 1993). Depending on conditions, winter ice cover ranges from 0-100 percent of surface area (Bolsenga and Herdendorf 1993).

The lake is divided into eastern, central, and western basins (i.e., eastern, central, and western Lake Erie; Bolsenga and Herdendorf 1993, Haltuch and others 2000; Fig. 1A). The western basin is relatively small (4,837 km² surface area, 25 km³ volume), shallow (mean and maximum depth of 7.4 and 21 m, respectively; Fig. 1B), and the most biologically productive per unit area (Bolsenga and Herdendorf 1993). Thermal stratification in the western basin is only temporary due to frequent wind-driven mixing, whereas stable summer stratification occurs in remaining basins (Bolsenga and Herdendorf 1993). The rather flat-bottomed central basin is intermediate in size, depth (15,061 km² surface area, 305 km³ volume, mean and maximum depth of 18.5 and 39 m; Fig. 1B), and productivity, and experiences hypolimnetic oxygen declines during summer months (Bolsenga and Herdendorf 1993, Haltuch and others 2000, McGucken 2000). The large, deep eastern basin (5,836 km² surface area, 154 km³ volume, mean and maximum depth of 18.9 and 64 m; Fig. 1B) has the lowest summer temperatures and productivity, and experiences little if any hypolimnetic oxygen depletion (Bolsenga and Herdendorf 1993, Haltuch and others 2000, Carrick 2004).

Spatial variation in benthic algal assemblage structure is heavily influenced by temperature, light, water flow regime (such as current and wave action), depth, and substrate type, especially particle size and hardness (Lowe 1996, Wehr and Sheath 2003a). In Lake Erie, rock (i.e., bedrock, boulder, cobble) is the dominant substrate type in nearshore, or littoral regions of the eastern basin (Bolsenga and Herdendorf 1993, Haltuch and others 2000; Fig. 1C). Rock is also abundant along the south shore of the central basin, and in the island region of the western basin (Bolsenga and Herdendorf 1993, Haltuch and others 2000; Fig. 1C). Remaining substrate generally consists of clay, mud, sand, or gravel; although abundant glacial till along north shores of eastern and central basins, and southwest shores of the central and western basins, contains particles ranging from large rocks to clay or mud (Bolsenga and Herdendorf 1993, Haltuch and others 2000). Overall, approximately 85 percent

of the lake bed is composed of soft substrate (i.e., fine sediments, including clay, mud, sand; Haltuch and others 2000).

RESULTS AND DISCUSSION

Macroalgae of Rocky Littoral Habitat

The most thoroughly studied benthic algal assemblage of Lake Erie consists of filamentous, colonial, and plantlike growth forms that are often visible to the unaided eye and are attached to hard substrates in shallow, nearshore locations (i.e., rocky littoral habitat). Bedrock, boulders, and cobble are primary substrates, although other large substrate particles (such as gravel, wood, concrete, metal) are also colonized. Most rocky littoral habitat in Lake Erie is located along exposed shorelines subject to heavy wave action and substantial water movement (Bolsenga and Herdendorf 1993, Haltuch and others 2000). Three filamentous genera have frequently been reported to dominate biomass and areal cover in this habitat: the rhodophyte *Bangia* and the chlorophytes *Cladophora* and *Ulothrix* (Garwood 1982, Chilton and others 1986, Higgins and others 2008; Table 1). Additional macroalgal genera recorded in multiple surveys or that have occasionally been very abundant include the cyanophytes *Calothrix*, *Lyngbya*, *Oscillatoria*, *Phormidium*, and *Plectonema*, the rhodophyte *Chroodactylon*, and the chlorophytes *Hydrodictyon*, *Rhizoclonium*, *Stigeoclonium*, and *Tetraspora* (Pieters 1902, Taft 1964, Taft and Kishler 1968, Downing 1970, Taft and

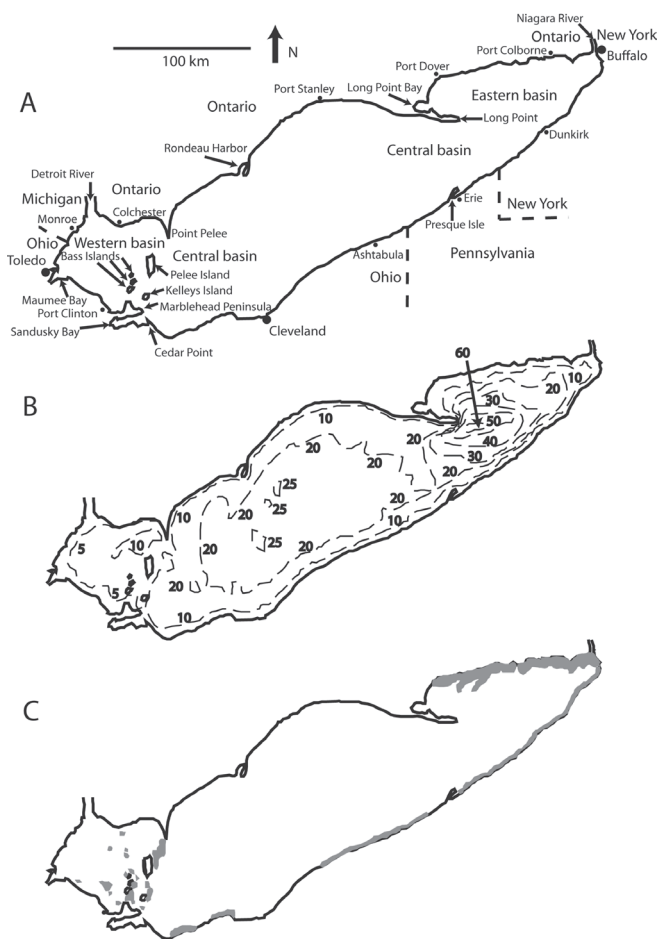


FIGURE 1. Lake Erie maps showing (A) key landmarks and other geographic locations, (B) depth contours (in m), and (C) bottom areas covered by rock substrate (indicated by gray shading). Maps were constructed using information from Bolsenga and Herdendorf (1993), Haltuch et al. (2000), and McGucken (2000).

TABLE 1

Published records of algae from Lake Erie benthic habitats, with accompanying ecological information, if provided.
Division and generic-level classification and nomenclature are from Webr and Sheath (2003b) and Lewis and McCourt (2004; Charophyta only).
For depths, WL = water line, AWL = above water line (with distance from water line in parentheses), and BWL = below water line with depth unspecified.
For basins, E = eastern, C = central, W = western.
A list of citations corresponding to numbered references is located at the bottom of this table.
Only references containing original records (i.e., first published accounts) are cited.

Genus (with number of reported species, if identified to that level)	Substrates	Depths (range in m)	Basins	Years recorded	References
Division Cyanophyta					
<i>Anabaena</i> Bory ex Bornet et Flahault	Rock, <i>Dreissena</i> shell	0.25 – 1	W	2004	19
<i>Aphanocapsa</i> Nägeli (1)			W	1971 or earlier	75
<i>Calothrix</i> Agardh ex Bornet et Flahault (3)	Rock, algae	AWL – 0.3	W	1967	18, 74-75
<i>Chamaesiphon</i> Braun et Grunow in Rabenhorst (1)	Algae (<i>Cladophora</i>)	AWL – 0.3	E, W	1967, 1977-1978	18, 33, 65
<i>Chlorogloea</i> Wille (1)	Rock	AWL – 0.3	W	1967	18
<i>Chroococcus</i> Nägeli (1)	Rock, <i>Dreissena</i> shell	0.25 – 1	W	1974, 2004	19-20
<i>Coelosphaerium</i> Nägeli (1)	Rock	0.25 – 0.5	W	2004	19
<i>Gloeotrichia</i> Agardh ex Bornet et Flahault (1)			W	1971 or earlier	75
<i>Gomphosphaeria</i> Kützing			W	1971 or earlier	75
<i>Hydrocoleum</i> Kützing (1)	Rock, concrete, wood	AWL – 0.3	W	1967	18
<i>Lyngbya</i> Agardh ex Gomont (9)	Rock, wood, algae (<i>Cladophora</i>)	AWL – 0.3	E, W	1898, 1965-1971, 1976-1978	18, 33, 61, 65, 76
<i>Merismopedia</i> Meyen (1)	Rock, <i>Dreissena</i> shell	0.25 – 1	W	1974, 2004	19-20
<i>Microcoleus</i> Desmazières ex Gomont (3)	Rock, wood	AWL – 0.3	W	1967	18
<i>Nostoc</i> Vaucher ex Bornet et Flahault (1)	Rock, wood	AWL – 0.3	W	1967	18
<i>Oscillatoria</i> Vaucher ex Gomont (10)	Rock, wood, algae (<i>Cladophora</i>), <i>Dreissena</i> shell	AWL(0.5) – 3	E, W	1965-1971, 1974, 1976-1980, 2004	18-20, 33, 42, 65, 75-76
<i>Phormidium</i> Kützing ex Gomont (5)	Rock, algae (<i>Cladophora</i>)	AWL – 2.5	W	1965-1971, 1979-1980	18, 42, 76
<i>Plectonema</i> Thuret ex Gomont (1)	Rock, algae (<i>Cladophora</i> , <i>Chara</i>)	0.6 – 5.2	W	1938-1941, 1965-1971, 1979-1980	42, 71, 76
<i>Schizothrix</i> Kützing ex Gomont (7)	Rock, wood, fine sediment, algae (<i>Cladophora</i> , <i>Stigeoclonium</i>)	AWL – 25	C, W	1967, 1970	9, 18
<i>Spirulina</i> Turpin ex Gomont	Rock	0.25 – 0.5	W	2004	19
<i>Tolypothrix</i> Kützing ex Bornet et Flahault (2)	Rock, algae (<i>Cladophora</i>)	AWL	W	1967, 1977-1978	18, 65, 75
Division Rhodophyta					
<i>Bangia</i> Lyngbye (1)	Rock, boulder, concrete, firm substrate, algae (<i>Cladophora</i>)	AWL(2) – 3	E, C, W	1964, 1969, 1975-1982, 1995	14, 21, 33-34, 41-42, 53, 64-67, 77, 84
<i>Batrachospermum</i> Roth	Gastropod shell	W			75
<i>Chroodactylon</i> (= <i>Asterocystis</i>) Hansgirg (1)	Rock, algae (<i>Cladophora</i>)	AWL – 0.3	E, C, W	1964-1971, 1975, 1977-1982	18, 65, 68, 73, 75-77

TABLE 1 (cont.)

Genus (with number of reported species, if identified to that level)	Substrates	Depths (range in m)	Basins	Years recorded	References
Division Chlorophyta					
<i>Ankistrodesmus</i> Corda (1)	<i>Dreissena</i> shell	1	W	1974, 2004	19-20
<i>Apatococcus</i> (= <i>Protococcus</i>) Brand em. Geitler (1)	Algae	AWL – 0.3	W	1967	18
<i>Aphanochaete</i> Braun (2)	Algae (<i>Cladophora</i> , <i>Oedogonium</i> , <i>Tribonema</i>)	AWL – 0.3	W	1927-1936, 1967	18, 75, 78
<i>Apiocystis</i> Nägeli (1)	Algae, vascular plants		W	1971 or earlier	75
<i>Bulbochaete</i> Agardh (5)			W	1971 or earlier	75
<i>Chaetophora</i> Schrank (3)			W	1971 or earlier	75
<i>Chaetosphaeridium</i> Klebahn (1)	Algae		W	1927-1936	75, 78
<i>Characiopsis</i> Borzi			W	1971 or earlier	75
<i>Characium</i> Braun (1)	Algae, vascular plants		W	1971 or earlier	75
<i>Chlamydomonas</i> Ehrenberg (1)	Sand	AWL – WL	E, C, W	1902-1906	31, 38
<i>Cladophora</i> Kützing (2)	Rock, (bedrock, boulder, cobble, gravel) concrete, wood, dock, vascular plants, <i>Dreissena</i> shells	AWL(0.9) – 10	E, C, W	1865-1907, 1919-1983, 1995-2002, 2004, 2006	1-5, 13-14, 16-29, 32- 34, 37-40, 42-52, 54- 65, 68, 70, 74-78, 80-86
<i>Closterium</i> Nitzsch ex Ralfs (1)	Rock	0.25 – 0.5	W	1974, 2004	19-20
<i>Coelastrum</i> Nägeli (1)			W	1974	20
<i>Coleochaete</i> Brébisson (4)	Vascular plants	BWL – 0.3	W	1927-1936, 1967	18, 75, 78
<i>Cosmarium</i> Corda ex Ralfs (5)	Rock, concrete, fine sediment, vascular plants	0.25 – 25	C, W	1898, 1965-1971, 1974, 2004	9, 19-20, 61, 76
<i>Crucigenia</i> Morren (1)			W	1974	20
<i>Cylindrocystis</i> Meneghini ex De Bary (1)	Rock	WL	W	1938-1941	72
<i>Dichotomosiphon</i> Ernst (1)			W	1971 or earlier	75
<i>Dimorphococcus</i> Braun	<i>Dreissena</i> shell	1	W	2004	19
<i>Draparnaldia</i> Bory de St. Vincent (1)			W	1927-1936	75, 78
<i>Elakatothrix</i> Wille (1)	Vascular plants			1928 or earlier	15
<i>Gloeochaete</i> Lagerheim (1)			W	1971 or earlier	75
<i>Gloeocystis</i> Nägeli (1)	Dock		W	1964 or earlier	73
<i>Gongrosira</i> Kützing (1)	Algae (<i>Cladophora</i>)	0.5	W	1965-1971	74-76
<i>Haematococcus</i> Agardh (1)	Rock	AWL	W	1967	18
<i>Hydrodictyon</i> Roth	Rock	0.25 – 0.5	W	2004	19
<i>Klebsormidium</i> (= <i>Hormidium</i>) Silva, Mattox et Blackwell (1)	Rock, wood	AWL – 0.3	W	1967	18
<i>Microspora</i> Thuret (2)		< 3	E, W	1976-1977	33, 75

TABLE 1 (cont.)

Genus (with number of reported species, if identified to that level)	Substrates	Depths (range in m)	Basins	Years recorded	References
<i>Mougeotia</i> Agardh		< 3	E	1976-1978	33
<i>Oedogonium</i> Link (18)	Fine sediment, vascular plants	BWL – 25	E, C, W	1898, 1927-1936, 1970, 1974, 1976-1978	7, 9, 20, 33, 61, 75, 78
<i>Oocystis</i> Braun	Fine sediment, <i>Dreissena</i> shell	1 – 25	C, W	1970, 2004	7, 9, 19
<i>Pandorina</i> Bory de St. Vincent	Rock, <i>Dreissena</i> shell	0.25 – 1	W	2004	19
<i>Pediastrum</i> Meyen (2)	Rock, fine sediment, <i>Dreissena</i> shell	0.25 – 60	E, C, W	1970, 1974, 1997-1998, 2004	9, 11, 19-20
<i>Rhizoclonium</i> Kützing (2)	Rock, metal	AWL – 0.3	W	1927-1936, 1965-1971	18, 75-76, 78
<i>Scenedesmus</i> Meyen (4)	Rock, fine sediment, <i>Dreissena</i> shell	0.25 – 25	C, W	1970, 1974, 2004	9, 19-20
<i>Schizomeris</i> Kützing (1)	Dock		W	1971 or earlier	75
<i>Sphaerocystis</i> Chodat	Fine sediment	20 – 25	C	1970	9
<i>Spirogyra</i> Link	Algae (<i>Cladophora</i>), vascular plants	< 3	E, W	1898, 1974, 1976-1978, 2002	20, 28, 33, 61
<i>Staurostrum</i> Meyen ex Ralfs (1)	Fine sediment, vascular plants	20 – 25	C, W	1898, 1970	7, 9, 61
<i>Stigeoclonium</i> Kützing (9)	Rock, fine sediment, algae (<i>Cladophora</i>), vascular plants	AWL(0.2) – 20	E, C, W	1927-1936, 1965-1971, 1974-1976, 1978-1980, 2002, 2004	12, 18-20, 33, 42, 75-78
<i>Stylosphaeridium</i> Geitler et Gimesi (1)	Algae (<i>Coelosphaerium</i>)		W	1971 or earlier	75
<i>Tetraedron</i> Kützing	Fine sediment	20 – 25	C	1970	9
<i>Tetraspora</i> Link (2)	Rock, algae (<i>Cladophora</i>)	AWL(0.2) – 1.3	W	1965-1971, 1974-1975, 1979-1980	18, 20, 42, 75-77
<i>Trentepohlia</i> Martius (1)	Rock	AWL – 0.3	W	1967	18, 73, 75
<i>Ulothrix</i> Kützing (4)	Rock (bedrock), dock	AWL(1) – 1.5	E, W	1917 or earlier, 1950-1951, 1965-1973, 1975-1980	18, 21, 33, 42, 44, 49, 52, 68, 73, 75-77, 79, 81, 83-85
<i>Uronema</i> Lagerheim (1)	Algae (<i>Cladophora</i> , <i>Hydrodictyon</i>)	AWL – 0.3	W	1967	18
<i>Westella</i> de Wildeman (1)			W	1974	20
<i>Zygnema</i> Agardh		< 3	E, W	1974, 1976-1978	20, 33
Division Charophyta					
<i>Chara</i> Linnaeus (11)	Gravel, sand, clay, mud	0.05 – 3	E, C, W	1898, 1900, 1905-1906, 1938-1941, 1962, 1976, 1991-1992, 1995	6, 10, 31, 35-36, 61, 71, 87
<i>Nitella</i> Agardh (5)	Sand, mud	0.3 – 0.6	E, W	1898, 1962, 1991-1992, 1995	6, 36, 61
<i>Tolypella</i> Braun (1)			W	1898	61
Division Euglenophyta					
<i>Colacium</i> Ehrenberg (2)	Boat landing, copepod exoskeleton		W	1902-1904	38
<i>Euglena</i> Ehrenberg (4)	Vascular plants		W	1902-1904	38

TABLE 1 (cont.)

Genus (with number of reported species, if identified to that level)	Substrates	Depths (range in m)	Basins	Years recorded	References
<i>Phacus</i> Dujardin (6)	Vascular plants		W	1902-1904, 1974	20, 38
<i>Trachelomonas</i> Ehrenberg (3)	Algae (filamentous), vascular plants, <i>Dreissena</i> shell	1	W	1898, 1902-1904, 2004	19, 30, 38
Division Tribophyta					
<i>Gleobotrys</i> Pascher (1)			W	1971 or earlier	75
<i>Peroniella</i> Gobi (1)	Algae (<i>Oedogonium</i>)		W	1971 or earlier	75
<i>Tribonema</i> Derbes et Solier	Fine sediment	20 – 25	C	1970	7-9
<i>Vaucheria</i> de Candolle (1)	Sand	0.6	W	1898	61
Division Chrysophyta					
<i>Dinobryon</i> Ehrenberg (1)	Vascular plants		W	1898, 1902-1904	30, 38
<i>Stylobryon</i> Fromentel (1)	Vascular plants		W	1902-1904	38
Division Synurophyta					
<i>Mallomonas</i> Perty (2)	Algae		W	1902-1904, 1974	20, 38
Division Bacillariophyta					
<i>Achnanthes</i> Bory	Algae (<i>Cladophora</i>)		W	1965-1971	76
<i>Achnanthidium</i> Kützing	Rock	0.25 – 0.5	W	2004	19
<i>Actinocyclus</i> Ehrenberg (1)	Fine sediment	20	C	2002	12
<i>Amphora</i> Ehrenberg ex Kützing	Rock	0.25 – 0.5	W	2004	19
<i>Aulacoseira</i> Thwaites (1)	Fine sediment	10 – 60	E, C	1997-1998, 2002	11-12
<i>Cocconeis</i> Ehrenberg (2)	Rock, algae (<i>Cladophora</i>), <i>Dreissena</i> shell	0.25 – 3	E, C, W	1965-1971, 1976-1980, 2004	5, 19, 33, 42, 52, 65, 76
<i>Cyclotella</i> Kützing ex Brébisson (2)	Rock, fine sediment, <i>Dreissena</i> shell	0.25 – 60	E, W	1997-1998, 2004	11, 19
<i>Cymbella</i> Agardh (1)	Algae (<i>Cladophora</i>)	< 3	E, W	1965-1971, 1976-1978	33, 65, 76
<i>Diatoma</i> Bory de St. Vincent (1)	Rock	0.25 – 0.5	W	2004	19
<i>Epithemia</i> Brébisson (1)	Fine sediment	10 – 60	E	1997-1998	11
<i>Eunotia</i> Ehrenberg (1)	Rock	0.25 – 0.5	W	2004	19
<i>Fragilaria</i> Lyngbye (1)	Rock, fine sediment, <i>Dreissena</i> shell	0.25 – 20	C, W	2002, 2004	12, 19
<i>Gomphonema</i> Ehrenberg	Algae (<i>Cladophora</i>), <i>Dreissena</i> shell	1	E, W	1976, 1978, 2004	19, 33
<i>Gyrosigma</i> Hassall	Rock, algae (<i>Cladophora</i>), <i>Dreissena</i> shell	0.25 – 1	W	1965-1971, 2004	19, 76
<i>Melosira</i> Agardh	Rock, <i>Dreissena</i> shell	0.25 – 1	W	2004	19
<i>Navicula</i> Bory (1)				1978 or earlier	69
<i>Nitzschia</i> Hassall (1)	Rock, fine sediment, <i>Dreissena</i> shell	0.25 – 60	E, W	1997-1998, 2004	11, 19
<i>Pleurosigma</i> Smith (1)	Fine sediment	10 – 60	E	1997-1998	11
<i>Rhoicosphenia</i> Grunow (1)	Rock, algae (<i>Cladophora</i>)	0.25 – 3	E, W	1965-1971, 1976-1980, 2004	19, 33, 42, 52, 65, 76

TABLE 1 (cont.)

Genus (with number of reported species, if identified to that level)	Substrates	Depths (range in m)	Basins	Years recorded	References
<i>Rhopalodia</i> Müller	Rock	0.25 – 0.5	W	2004	19
<i>Stephanodiscus</i> Ehrenberg (3)	Fine sediment	10 – 60	E, C	1997-1998, 2002	11-12
<i>Surirella</i> Turpin	Rock, <i>Dreissena</i> shell	0.25 – 1	W	2004	19
<i>Synedra</i> Ehrenberg	Rock, <i>Dreissena</i> shell	0.25 – 1	W	2004	19
Division Pyrrophyta					
<i>Peridiniopsis</i> (= <i>Glenodinium</i>) Lemmermann (1)			W	1974	20
<i>Peridinium</i> Ehrenberg (1)	Vascular plants		W	1898	30
Division Cryptophyta					
<i>Chilomonas</i> Ehrenberg (2)	Vascular plants		W	1902-1904	38
<i>Cryptomonas</i> Ehrenberg (1)	Vascular plants		W	1902-1904	38

1. Barton and Hynes 1976; 2. Barton and Hynes 1978a; 3. Barton and Hynes 1978b; 4. Barton and others 2005; 5. Bellis and McClarty 1967; 6. Berst and McCrimmon 1966; 7. Braidech and others 1972; 8. Burns and Ross 1972a; 9. Burns and Ross 1972b; 10. Burr 1901; 11. Carrick 2004; 12. Carrick and others 2005; 13. Charlton and others 2000; 14. Chilton and others 1986; 15. Collins 1928; 16. Davies and Hecky 2005; 17. Dermott and others 1998b; 18. Downing 1970; 19. Duggan and Francouer 2007; 20. Frederick 1975; 21. Garwood 1982; 22. Gerloff and Fitzgerald 1976; 23. Hecky and others 2004; 24. Herbst 1969; 25. Higgins and others 2005a; 26. Higgins and others 2005b; 27. Higgins and others 2006; 28. Higgins and others 2008; 29. Howell 1998; 30. Jennings 1899; 31. Jennings 1909; 32. Judd 1975; 33. Kirby and Dunford 1981; 34. Kishler and Taft 1970; 35. Knapton and Pauls 1994; 36. Knapton and Petrie 1999; 37. Kreckler and Lancaster 1933; 38. Landacre 1908; 39. Langlois 1954; 40. Limén and others 2005; 41. Lin and Blum 1977; 42. Lorenz and Herdendorf 1982; 43. Lorenz and others 1991; 44. Mantai 1974; 45. Mantai and Haase 1977; 46. Mantai 1978; 47. Mantai and others 1982; 48. Mantai 1987; 49. McMillan and Verduin 1953; 50. Millner and Sweeney 1982; 51. Millner and others 1982; 52. Moore 1978; 53. Müller and others 1998; 54. Neil and Owen 1964; 55. Neil 1975b; 56. Neil 1975c; 57. Neil and Jackson 1982; 58. Painter and Jackson 1989; 59. Palmer 1977; 60. Patterson and others 2005; 61. Pieters 1902; 62. Poston and Gamet 1964; 63. Ratti and Barton 2003; 64. Sheath and Cole 1980; 65. Sheath and Morison 1982; 66. Sheath 1984; 67. Sheath and Cole 1984; 68. Sheath 1987; 69. Stevenson and Stoermer 1978; 70. Storr and Sweeney 1975; 71. Taft 1942; 72. Taft 1945; 73. Taft 1964; 74. Taft and Kishler 1968; 75. Taft and Taft 1971; 76. Taft and Kishler 1973; 77. Taft 1975; 78. Tiffany 1937; 79. Transeau 1917; 80. van Overdijk and others 2003; 81. Verduin 1952; 82. Verduin 1969; 83. Verduin 1972; 84. Wolfe and Sweeney 1982; 85. Wood 1968; 86. Wood 1975; 87. Wood 1947

Taft 1971, Taft and Kishler 1973, Taft 1975, Kirby and Dunford 1981, Lorenz and Herdendorf 1982, Duggan and Francouer 2007; Table 1). The cyanophytes *Anabaena*, *Hydrocoleum*, *Microcoleus*, *Nostoc*, *Schizothrix*, *Spirulina*, and *Tolypothrix*, and the chlorophytes *Cylindrocystis*, *Klebsormidium*, and *Trentepohlia* have also been recorded from rocky littoral habitat of Lake Erie (Taft 1945, Taft 1964, Downing 1970, Duggan and Francouer 2007; Table 1).

Macroalgal Ecology in Rocky Littoral Habitat

Several studies of rocky littoral macroalgae in Lake Erie focused on *Bangia*, *Cladophora*, and *Ulothrix* (Table 1). *Bangia* has origins in European freshwater ecosystems, was initially reported from eastern Lake Erie in 1964, and colonized all Lake Erie basins by 1982 (Lin and Blum 1977, Sheath 1984, Sheath 1987, Müller and others 1998). A systematics analysis indicated that one species, *B. atropurpurea*, inhabits the North American Great Lakes (Sheath and Cole 1984). Two *Cladophora* species have been reported from Lake Erie (*C. fracta* and *C. glomerata*), although at present there is widespread thought that only *C. glomerata* actually inhabits this ecosystem (Taft 1975, Higgins and others 2008; Table 1). Bailey's (1847) report of *C.* (= *Conferva*) *glomerata* appears to be the earliest published record of any algal species from Lake Erie, and *Cladophora* records from Lake Erie rocky littoral habitat date back to at least 1865 (Taft and Kishler 1973). *Ulothrix* was found in Lake Erie benthic habitat in the early 1900s (Transeau 1917). Four *Ulothrix* species have been recorded from the lake, with *U. zonata* most often reported (Downing 1970, Taft and Taft 1971, Garwood

1982; Table 1). Both *Cladophora* and *Ulothrix* inhabit marine ecosystems, and it has been hypothesized that, like *Bangia*, these genera invaded the North American Great Lakes after European settlement of the region (Sheath and Morison 1982, Sheath 1987). Invasion of Lake Erie benthic habitats by *Bangia*, *Cladophora*, *Ulothrix*, and the marine rhodophyte *Chroodactylon ramosum* was hypothesized to be enabled by increased halide concentrations in the lake following industrialization of the watershed (Garwood 1982, Sheath and Morison 1982, Sheath 1987). However, there is no consensus that *Cladophora* and *Ulothrix* are invasive. Both genera were recorded in early Lake Erie algal surveys, and *Cladophora* has even been suspected of inhabiting glacial lakes that preceded modern Lake Erie (Bailey 1847, Transeau 1917, Taft and Kishler 1973, Sheath 1987).

Investigations demonstrated spatial and seasonal differences in distribution, abundance, and growth among rocky littoral macroalgae in Lake Erie. Surveys of wave-washed shoreline revealed *Ulothrix* as a dominant macroalga from the splash zone (up to 1 m above the water line) to a depth of 1.5 m from late fall through early spring (Garwood 1982, Lorenz and Herdendorf 1982). *Bangia* has been recorded from 2 m above to at least 1 m below the water line, and was found to be most abundant in May-June when it often co-dominated the macroalgal assemblage with *Ulothrix* and *Cladophora* (Garwood 1982, Sheath 1987). From early- to mid-summer, *Cladophora* has typically dominated the assemblage, being recorded at depths of 0.9 m above to 10 m below the water line (Taft and Kishler 1973, Garwood 1982, Higgins and others 2005a,b).

Cladophora abundance has generally been found to be lowest from December–April, consisting of holdfasts or short filaments (Taft and Kishler 1973, Lorenz and Herdendorf 1982). Growth was observed to begin in April with filaments readily apparent from May–July, followed by significant detachment (i.e., sloughing) and biomass loss from June–August, substantial regrowth in September–October, and declining abundance thereafter (Garwood 1982, Higgins and others 2005a,b, Higgins and others 2006).

Lake Erie-based investigations provided evidence that temperature, light, nutrient availability, intra- and interspecific competition, and differential tolerance of dessication and wave stress were causes for spatial and seasonal variation in macroalgal abundance. Temperatures at which *Ulothrix* (range = 0–15°C), *Bangia* (2–26°C), and *Cladophora* (5–23°C) grew in laboratory and field studies were consistent with seasonal abundance fluctuations in Lake Erie (Garwood 1982, Higgins and others 2005a, Higgins and others 2008). Similarly consistent with relative abundance periodicities were findings that maximum photosynthetic rate for *Ulothrix* occurred at a lower temperature (4°C) than *Cladophora* (17°C), and that *Ulothrix* was more sensitive to photoinhibition than *Cladophora* (McMillan 1951 in Wolfe and Sweeney 1982, McMillan and Verduin 1953). Studies focused on *Cladophora* revealed cell break down before summer sloughing, with likely causes including energetic stress due to high water temperature, self-shading by filaments that reduced photosynthetically active radiation (PAR) below critical levels, and phosphorus limitation due to sequestration in high algal biomass (Mantai 1987, Higgins and others 2006, Higgins and others 2008). Lorenz and others (1991) found negligible growth in Lake Erie *Cladophora* below a light intensity of 29 $\mu\text{E}/\text{m}^2/\text{s}$, suggesting that exposure to light at or above this level is necessary for substrate colonization and persistence. Although there is evidence for many nutrients occasionally limiting *Cladophora* growth in Lake Erie, phosphorus was determined to be the primary growth-limiting nutrient (Gerloff and Fitzgerald 1976, Higgins and others 2005b, Higgins and others 2008). Many studies revealed positive relationships between soluble phosphorus concentration and indicators of *Cladophora* production, including tissue phosphorus concentration, photosynthetic rate, and cell growth rate (Neil and Jackson 1982, Painter and Jackson 1989, Higgins and others 2005b).

Physical interactions among taxa have also been found to affect macroalgal assemblage structure in rocky littoral habitat. Sheath (1987) concluded that competitive exclusion was the cause for absence of *Ulothrix* in habitat invaded by *Bangia* in one survey. But in another Lake Erie study, *Bangia* and *Ulothrix* coexisted in rocky habitat from late spring to early summer (Garwood 1982). Similarly, Garwood (1982) found *Bangia* and *Cladophora* co-inhabiting rock in eastern Lake Erie in late spring, but concluded that *Cladophora* outcompeted and eliminated *Bangia* from a zone extending from 0.5 m above to 1 m below the water line by mid-summer. However, *Bangia*'s apparently superior tolerance of dessication and physical disturbance enabled summer survival above the water line and along heavily wave-scoured shorelines where *Cladophora* could not survive (Taft 1975, Sheath and Cole 1980, Garwood 1982, Lorenz and Herdendorf 1982, Wolfe and Sweeney 1982). Seasonal declines in abundance of typically dominant genera may also enable periodic dominance by other macroalgal genera. Significant growth of *Stigeoclonium* was observed to succeed *Ulothrix* and precede *Cladophora* growth in the spring, and *Tetraspora* was reported covering rock vacated by detached *Cladophora* in mid-summer (Taft and Kishler 1973, Taft 1975,

Lorenz and Herdendorf 1982). Extensive beds of *Plectonema* were also found to persist during periods of high *Cladophora* abundance by occurring at depths where light was insufficient to support *Cladophora* (Taft and Kishler 1973).

Whereas competition and habitat partitioning have likely played important roles in structuring rocky littoral macroalgal assemblages in Lake Erie, these macroalgae have also benefited other organisms by providing food and habitat. *Cladophora*, *Hydrodictyon*, and *Stigeoclonium* were reported to support algal epiphytes in Lake Erie (Table 1). By increasing benthic habitat area and complexity, *Cladophora* in particular has functioned as a key community structuring agent, indirectly influencing food web structure and functions (Lowe 1996, Higgins and others 2008). *Cladophora*'s stable cell wall has been found to support high densities and diversity of associated algae (Lorenz and Herdendorf 1982, Chilton and others 1986, Higgins and others 2008). This review uncovered 21 algal genera that were reported to be physically associated with *Cladophora* as epiphytes (i.e., firmly attached) or metaphytes (i.e., in contact with but not firmly attached) in Lake Erie (Table 1). Similarly, very high invertebrate densities on *Cladophora*-covered rock in Lake Erie were hypothesized to result from refuges filaments provide from predation, and food in the form of highly nutritious diatom epiphytes and, to a lesser extent, *Cladophora* itself (Chilton and others 1986, Lowe 1996, Van Overdijk and others 2003, Duggan and Francouer 2007).

Environmental Change and Cladophora in Lake Erie

No Lake Erie alga, planktonic or benthic, has received more attention than *Cladophora*, nor has any taxon served as a better indicator of environmental conditions in the lake (Shear and Konasewich 1975, Higgins and others 2008). Although *Cladophora* has beneficial ecological functions, these have generally been overlooked in Lake Erie due to frequent unnaturally high abundance levels and associated problems. Temporal change in *Cladophora* abundance has been associated with three historical events in Lake Erie, 1) eutrophication associated with increased anthropogenic activity in the watershed, 2) oligotrophication following the 1972 Great Lakes Water Quality Agreement, and 3) the mid-1980s invasion by *Dreissena* mussels. Inputs of pollutants to Lake Erie increased after Europeans colonized the watershed in the 1700s and converted a predominantly forested terrestrial landscape to farmland and urban centers (Stoermer and others 1996, Leach 1999). Macroscopic algal accumulations, presumably dominated by *Cladophora*, were recorded along the western Lake Erie shoreline by 1820 and served as an early indicator of eutrophication (Taft and Kishler 1973, Shear and Konasewich 1975). From 1927–1936, Tiffany (1937) reported *Cladophora* as widespread on hard substrates of western Lake Erie, and noted occasional floating masses. By the 1930s, health agencies received regular complaints of detached *Cladophora* accumulating on shorelines across Lake Erie (Neil and Owen 1964). Taft and Kishler (1973) reported noticeable increases in *Cladophora* abundance in western Lake Erie after World War II. In the 1960s, Verduin (1969) remarked that *Cladophora* abundance in eastern and western Lake Erie was increasing enormously, and Taft and Kishler (1973) reported 100% increase in *Cladophora* biomass in western Lake Erie from 1965–1966.

By the 1960s, summer *Cladophora* shoreline accumulations up to 15 m wide and 0.6 m deep were regular occurrences (Herbst 1969, Neil 1975a). Shoreline fouling in the 1960s and 1970s reduced waterfront property values by up to 80–85 percent, and

decomposing *Cladophora* on swimming beaches produced strong odors, high coliform counts, abundant insects, and concern that bathers would become entangled in drifting algae and drown (Herbst 1969, Neil 1975a). Water intake screens were clogged by filaments, algal-related tastes and odors in drinking water supplies were attributed to decomposing *Cladophora*, and fouled boat hulls and nets adversely affected watercraft navigation and fishing operations (Poston and Gamet 1964, Herbst 1969, Taft and Kishler 1973). Bacterially-mediated decomposition of detached *Cladophora* that settled in offshore and sheltered nearshore habitats likely contributed to benthic oxygen depletion (Taft and Kishler 1973, Neil and Jackson 1982).

By 1971, there was general consensus that eutrophication was the primary cause of *Cladophora*-related problems and Lake Erie's poor overall condition, and that reduced *Cladophora* abundance and improvement in water and habitat quality could only be achieved by reducing external nutrient loads, particularly phosphorus (Neil and Owen 1964, Taft and Kishler 1973, Shear and Konasewich 1975). The 1972 Great Lakes Water Quality Agreement, a legislative effort between Canada and the United States, sought to reverse eutrophication by reducing inputs of phosphorus and other pollutants (McGucken 2000, Munawar *et al.* 2002). Two of three goals in a 1978 revision of this agreement emphasized reducing *Cladophora* abundance (Shear and Konasewich 1975, McGucken 2000). By the mid-1970s, soluble phosphorus concentrations in Lake Erie began to decline (Charlton and others 2000, Higgins and others 2008). Nuisance levels of *Cladophora*, including heavy beach accumulations, were reported as late as 1980 (Lorenz and Herdendorf 1982, McGucken 2000). However, by the mid-1980s, declines in *Cladophora* abundance were recognized by the International Joint Commission (IJC, the Great Lakes Science Advisory Board organized by Canadian and USA governments) which reported that "*Cladophora* no longer caused the problem it once did" (McGucken 2000).

In the mid-1980s, *Dreissena* mussels (*D. polymorpha* and *D. bugensis*) invaded Lake Erie (Leach 1999). By the mid-1990s, *Dreissena* occurred in all basins at densities of 10,000 or more individuals/m² in many rocky littoral habitats, with lesser densities on soft substrate (i.e., fine sediments) to depths exceeding 30 m (Dermott and others 1998a, Leach 1999). Summer *Cladophora* windrows reappeared on shorelines of all Lake Erie basins in the mid-1990s, with accumulations similar to those predating the Great Lakes Water Quality Agreement (Howell 1998, Charlton and others 2000, Higgins and others 2005b). Charlton and others (2000) classified eastern basin shoreline habitat as ecologically impaired in 1995 due to *Cladophora* fouling.

Cladophora surveys at shallow rocky sites in eastern Lake Erie confirmed that biomass per unit substrate area was greater in 1995-2006 than in 1985, and similar to biomass recorded in 1979-1980 (Howell 1998, Higgins and others 2006). Expansion of colonizable habitat also contributed to increased biomass on a lakewide scale (Higgins and others 2006). *Cladophora* occurred at depths of 10 m in 2002, exceeding maximum depths recorded before the Great Lakes Water Quality Agreement (4.3 m), and after pollution abatement but prior to the mussel invasion (7 m; Neil and Owen 1964, Lorenz and others 1991, Higgins and others 2006). Results from observational studies, experiments, and predictive modeling suggested that *Dreissena* stimulated the *Cladophora* resurgence, with likely mechanisms including increased benthic light and nutrient availability due to phytoplankton consumption and waste production by mussels (Hecky and others 2004, Higgins

and others 2005a, Higgins and others 2006). At post-*Dreissena* invasion abundance levels, respiring and decomposing *Cladophora* were found capable of depleting benthic oxygen in littoral habitats, and declining benthic invertebrate diversity at one Lake Erie site was blamed on habitat degradation by massive *Cladophora* growth (Ratti and Barton 2003, Davies and Hecky 2005).

Microalgae of Rocky Littoral Habitat

Exclusive of epiphytes, metaphytes, or epizoites, there is little published information for typically microscopic algae from hard substrate in Lake Erie. The chlorophyte *Gloeocystis* and the euglenoid *Colacium* were recorded from docks in early surveys of western Lake Erie (Landacre 1908, Taft 1964; Table 1). Downing (1970) recorded the cyanophyte *Chlorogloea* from wave-washed rock under a layer of filamentous algae, and the chlorophyte *Haematococcus* from rock pools above the water line. In western Lake Erie in the 1960s, Taft and Kishler (1973) found denuded rocks developing a covering of the chlorophyte genus *Cosmarium* after mid-summer *Cladophora* die-offs. Taft and Kishler (1973) also found rocks with silt accumulations supporting the diatom *Gyrosigma*. In a 2004 survey of littoral rocky habitat in western Lake Erie, Duggan and Francoeur (2007) recorded the cyanophytes *Chroococcus*, *Coelosphaerium*, and *Merismopedia*, the chlorophytes *Closterium*, *Cosmarium*, *Pandorina*, *Pediastrum*, and *Scenedesmus*, and the diatoms *Achnanthes*, *Amphora*, *Cocconeis*, *Cyclotella*, *Diatoma*, *Eunotia*, *Fragilaria*, *Gyrosigma*, *Melosira*, *Nitzschia*, *Rhoicosphenia*, *Rhopalodia*, *Surirella*, and *Synedra*. However, samples of Duggan and Francoeur (2007) were collected from *Cladophora*-covered rock, and the possibility that some of these genera were primarily or exclusively epiphytic or metaphytic cannot be ruled out.

Algae Inhabiting Soft Substrate in Littoral Habitat

Similar to *Cladophora* of rocky littoral habitat, temporal shifts in abundance of macroscopic charophytes inhabiting soft substrate have reflected environmental change in Lake Erie. In an 1898 survey of shallow habitat in western Lake Erie, Pieters (1902) recorded *Chara*, *Nitella*, and the only published record found for *Tolypella* (Table 1). In surveys conducted from 1900-1941, *Chara* was abundant and widespread at shallow depths (0.5-1.5 m) in sheltered bays and harbors throughout the lake (Burr 1901, Jennings 1909, Taft 1942, Wood 1947). In 1962, Berst and McCrimmon (1966) reported *Chara* to be the most abundant macrophyte on the mud bed of Long Point Bay, eastern Lake Erie.

However, no charophytes were found in western Lake Erie surveys from 1963-1973, even at locations where *Chara* and *Nitella* were formerly abundant (Pieters 1902, Wood 1947, Taft and Kishler 1973). Smith (1979 in Knapton and Petrie 1999) found *Chara* still present in Long Point Bay in a 1976 survey, but at lower abundance than in Berst and McCrimmon's (1966) 1962 survey. *Nitella* was not recorded from Long Point Bay in 1976, although it occurred there in 1962 (Berst and McCrimmon 1966, Smith 1979 in Knapton and Petrie 1999). These apparent *Chara* and *Nitella* declines were attributed to reduced water clarity and possible growth inhibition by elevated soluble phosphorus concentrations (Knapton and Petrie 1999). Support for the former hypothesis was provided by a 1991-1995 survey of Long Point Bay that documented recolonization and increased abundance of *Nitella* and *Chara* after post-*Dreissena* invasion increase in water clarity (Knapton and Petrie 1999).

In another study documenting changing algal assemblages, Frederick (1975) compared 1974 survey results from East Harbor, western Lake Erie, to earlier survey results from this harbor

dominated by soft substrate. Macro- and microscopic genera previously reported from benthic substrate that were not recorded in 1974 include the cyanophytes *Gomphosphaeria* and *Tolypothrix*, the chlorophytes *Bulbochaete*, *Chaetophora*, *Dichotomosiphon*, *Microspora*, *Rhizoclonium*, and *Schizomeris*, the charophytes *Chara* and *Nitella*, and the tribophyte *Vaucheria* (Pieters 1902, Tiffany 1937, Wood 1947, Taft and Taft 1971; Table 1). Dredging and deepening of the harbor in the 1960s, and associated shallow habitat loss, was hypothesized to be the primary cause for absence of many genera in 1974 (Frederick 1975). Reports of the chlorophyte *Chlamydomonas* from sand at and above the waterline in western Lake Erie were among the few additional published records found for microalgae on soft substrate in littoral habitat (Landacre 1908, Jennings 1909).

Epiphytic, Metaphytic, and Epizoid Algae *Algae Associated with Cladophora*

Epiphytic and metaphytic assemblages of *Cladophora* in Lake Erie have been relatively well described. The cyanophytes *Chamaesiphon* and *Lyngbya*, the rhodophyte *Chroodactylon*, the chlorophyte *Gongrosira*, and the diatoms *Cocconeis*, *Cymbella*, and *Rhoicosphenia* are the most frequently reported *Cladophora* associates (Bellis and McClarty 1967, Taft and Kishler 1968, Downing 1970, Taft and Taft 1971, Taft and Kishler 1973, Moore 1978, Kirby and Dunford 1981, Lorenz and Herdendorf 1982, Sheath and Morison 1982, Sheath 1987; Table 1). In a survey of several Lake Erie sites, Bellis and McClarty (1967) remarked that *Cocconeis* was almost always epiphytic on *Cladophora*. In their description of *Cladophora*-associated assemblages in Lake Erie, Taft and Kishler (1973) noted that *Cymbella* was the most common epiphyte in early spring, and as summer growth progressed, the diatoms *Achnanthes*, *Cocconeis*, and *Rhoicosphenia*, the cyanophytes *Lyngbya* and *Phormidium*, and the chlorophyte *Gongrosira* became abundant and eventually covered cell walls. In a *Cladophora* survey along the north shore of Lake Erie, Sheath and Morison (1982) found *Chamaesiphon* and *Lyngbya* accounting for 90% of epiphyte density. In late summer in western Lake Erie, Lorenz and Herdendorf (1982) found submerged *Cladophora* filaments to be completely covered with an algal assemblage dominated by *Cocconeis* and *Rhoicosphenia*, whereas *Cladophora* located above the water line had few epiphytes. Densities of *Cladophora* epiphytes, especially diatoms, have consistently been observed to increase from spring through summer, and competition with epiphytes for light and nutrients has been proposed as a contributing cause for mid-summer *Cladophora* die-offs (Taft and Kishler 1973, Moore 1978, Lorenz and Herdendorf 1982).

Several macroalgae have also been observed to become abundant *Cladophora* metaphytes during summer months, including the cyanophytes *Phormidium* and *Plectonema*, and the chlorophyte *Spirogyra* (Lorenz and Herdendorf 1982, Higgins and others 2008). The invasive rhodophyte *Chroodactylon ramosum* was first reported from Lake Erie in 1964 (Taft 1964, Sheath and Morison 1982). *Chroodactylon* has since been frequently reported as epiphytic on *Cladophora* at low densities, and was recorded at 10 of 15 Lake Erie sites in a 1982 survey (Downing 1970, Taft and Taft 1971, Taft and Kishler 1973, Sheath and Morison 1982, Sheath 1987; Table 1). Additional algae reported as epiphytic or metaphytic on *Cladophora* in Lake Erie include the cyanophytes *Oscillatoria*, *Schizothrix*, and *Tolypothrix*, the rhodophyte *Bangia*, the chlorophytes *Aphanochaete*, *Stigeoclonium*, *Tetraspora*, and *Uronema*, and the diatoms *Gomphonema* and *Gyrosigma* (Downing

1970, Taft and Kishler 1973, Kirby and Dunford 1981, Garwood 1982, Sheath and Morison 1982; Table 1).

Epiphytes of Other Algae and Vascular Plants

Additional algal genera and vascular plants are hosts for epiphytes and metaphytes in Lake Erie, although the ecology of these associations has not been well described. In rocky littoral habitat of Lake Erie, the cyanophytes *Calothrix* and *Schizothrix* were reported as epiphytes of unidentified algae and the chlorophyte *Stigeoclonium*, respectively, and the chlorophyte *Uronema* occurred on the chlorophyte *Hydrodictyon* (Taft and Kishler 1968, Downing 1970; Table 1). In unspecified benthic habitat, the chlorophyte *Aphanochaete* was epiphytic on the chlorophyte *Oedogonium* and the tribophyte *Tribonema*, and the tribophyte *Peroniella* was also epiphytic on *Oedogonium* (Taft and Taft 1971). Taft and Taft (1971) reported the chlorophyte *Stylosphaeridium* inhabiting the gelatinous envelope of planktonic *Coelosphaerium*. In benthic habitat dominated by soft substrate, the cyanophyte *Plectonema* was reported as epiphytic on *Chara*, and the chlorophytes *Apatococcus*, *Apiocystis*, *Chaetosphaeridium*, and *Characium*, the euglenoid *Trachelomonas*, and the synurophyte *Mallomonas* were recorded from unspecified algal taxa (Jennings 1899, Landacre 1908, Tiffany 1937, Taft 1942, Taft and Taft 1971; Table 1).

Soft substrate provides habitat for rooted, vascular plants that support diverse epiphytic and metaphytic algae. Genera recorded from plants in Lake Erie include the chlorophytes *Coleochaete*, *Cosmarium*, *Elakatothrix*, *Oedogonium*, *Spirogyra*, *Staurostrum*, and *Stigeoclonium*, the euglenoids *Euglena*, *Phacus*, and *Trachelomonas*, the chrysophytes *Dinobryon* and *Stylobryon*, the pyrophyte *Peridinium*, and the cryptophytes *Chilomonas* and *Cryptomonas* (Jennings 1899, Pieters 1902, Landacre 1908, Collins 1928, Tiffany 1937, Downing 1970, Taft and Taft 1971; Table 1). Kreeker and Lancaster (1933) also reported *Cladophora* as occasionally clinging to vegetation. Additionally, the chlorophytes *Apiocystis*, *Characium*, and *Coleochaete* were collected from plants in surveys of East Harbor, western Lake Erie (Tiffany 1937, Taft and Taft 1971). However, these genera were not recorded from the harbor in a subsequent 1974 survey, after benthic vegetation was eliminated due to habitat alteration (Frederick 1975).

Epizoid Algae

Few Lake Erie studies have reported algal genera attached to bodies of animals. Duggan and Francouer (2007) collected a large number of genera from shells of living *Dreissena* in Lake Erie, including the cyanophytes *Anabaena*, *Chroococcus*, *Merismopedia*, and *Oscillatoria*, the chlorophytes *Ankistrodesmus*, *Dimorphococcus*, *Oocystis*, *Pandorina*, *Pediastrum*, and *Scenedesmus*, the euglenoid *Trachelomonas*, and the diatoms *Cocconeis*, *Cyclotella*, *Fragilaria*, *Gomphonema*, *Gyrosigma*, *Melosira*, *Nitzschia*, *Surirella*, and *Synedra* (Table 1). Attached *Cladophora* has also been reported from *Dreissena* shells, and heavy growths have been hypothesized to adversely affect mussels by interfering with filter-feeding (Davies and Hecky 2005, Higgins and others 2005a,b). In other Lake Erie studies, the rhodophyte *Batrachospermum* was recorded from a gastropod shell, and the euglenoid *Colacium* from a copepod exoskeleton (Landacre 1908, Taft and Taft 1971).

Algae in Offshore and Deepwater Habitat

Surveys of habitat characterized by soft substrate in relatively deep (10–60 m) water produced records of living algae thought to

be of planktonic or nearshore benthic origins (Braidech and others 1972, Burns and Ross 1972a,b, Carrick 2004, Carrick and others 2005). In 1970 investigations of causes for increasing extent and duration of hypolimnetic anoxia in the central basin of Lake Erie, large quantities of physiologically active algae occurred on the lakebed at 20-25 m depths, including the cyanophyte *Schizothrix*, the chlorophytes *Cosmarium*, *Oedogonium*, *Oocystis*, *Pediastrum*, *Scenedesmus*, *Sphaerocystis*, *Staurostrum*, and *Tetraedron*, and the tribophyte *Tribonema* (Braidech and others 1972, Burns and Ross 1972a,b; Table 1). Authors hypothesized that high nutrient concentrations stimulated massive summer phytoplankton blooms, with algal fallout and subsequent respiration, death, and decomposition producing high hypolimnetic biological oxygen demand and oxygen depletion (Braidech and others 1972, Burns and Ross 1972c,d).

In the late 1990s, elimination of summer hypolimnetic anoxia in Lake Erie, particularly in the central basin, remained an unmet goal of the Great Lakes Water Quality Agreement (Carrick 2004, Carrick and others 2005). From 1997-2002, offshore surveys were conducted in all basins at depths ranging from 10-60 m to re-evaluate relationships between benthic algal communities and oxygen concentrations (Carrick 2004, Carrick and others 2005). The diatoms *Cyclotella* and *Stephanodiscus* dominated algal biomass, whereas the chlorophytes *Pediastrum* and *Stigeoclonium*, and the diatoms *Actinocyclus*, *Aulacoseira*, *Epithemia*, *Fragilaria*, *Nitzschia*, and *Pleurosigma* were also recorded (Carrick 2004, Carrick and others 2005; Table 1). Continued occurrence of high biomass suggested that algal respiration and decay still contributed to summer hypolimnetic anoxia in the central basin as of 2002 (Carrick 2004, Carrick and others 2005). However, species dominating total algal biomass (*Cyclotella comensis*, *Cyclotella ocellata*, *Stephanodiscus niagarae*) had only recently become abundant in Lake Erie after absence or reduced numbers dating back to 1900 (Stoermer and others 1996, Carrick 2004, Carrick and others 2005). Reestablishment of these species provided some evidence of oligotrophication since the early 1970s (Munawar and Munawar 1999, Carrick and others 2005).

CONCLUSIONS

Benthic algal taxa and assemblages that have been studied intensively have revealed much about environmental conditions in Lake Erie. In particular, study results have generated a reasonably solid understanding of how macroalgae in rocky littoral habitats regulate biological community structure through competitive interactions and habitat provision. Additionally, temporal shifts in abundance of *Cladophora* and charophytes in littoral habitats, and of diatoms in deepwater habitats, have provided clear evidence of environmental change in Lake Erie and insight into underlying mechanisms for such change.

However, significant information gaps remain. This review uncovered published records for 112 genera and 201 species of algae from benthic habitat of Lake Erie, but little accompanying ecological information for many taxa (Table 1). Information was notably lacking for microalgae in littoral habitat that were not epiphytes or metaphytes of other algae and plants. Microalgae are the foundation of nearshore benthic food webs, and by directing greater attention toward them our understanding of the Lake Erie ecosystem would be much improved. Modern surveys of rocky littoral macroalgal assemblages are also needed. Recent studies of these algae focused almost entirely on *Cladophora*, and the

abundance and ecological importance of other taxa under post-*Dreissena* invasion conditions are generally unknown.

Conditions in Lake Erie continue to change, and benthic algae will provide insight into ecological responses, and their consequences and causes. In 1993, Lake Erie was invaded by the round goby (*Neogobius melanostomus*), a fish that similar to *Dreissena* mussels, is native to the Ponto-Caspian region of Eurasia (MacIsaac 1999). Recent declines in *Dreissena* abundance in Lake Erie were attributed to goby predation (Barton and others 2005, Johnson and others 2005, Patterson and others 2005). Reduced abundance of *Cladophora* and other benthic algae in littoral habitat is a likely outcome of *Dreissena* declines due to reduced filter-feeding and associated declines in water clarity and benthic phosphorus availability (Hecky and others 2004, Barton and others 2005, Higgins and others 2005b, Johnson and others 2005). As of 2006, however, *Cladophora* was still exceedingly abundant in littoral habitat of Lake Erie (Barton and others 2005, Higgins and others 2008). Whatever the long-term outcome, interactions among *Neogobius*, *Dreissena*, and *Cladophora* will profoundly influence energy and nutrient flow pathways and community structure in Lake Erie (Vanderploeg and others 2002, Hecky and others 2004, Barton and others 2005).

Population explosion of metaphytic, filamentous cyanophytes is another emerging concern in Lake Erie, and may be a sign that the lake is again becoming increasingly eutrophic. Mid-summer blooms of *Lyngbya wollei* or *Plectonema wollei* were regular occurrences in the western basin from 2006-2008 (R.L. Lowe, unpublished data). Due to intraspecific variation in morphological taxonomic features, molecular analysis techniques are being used to determine whether *Lyngbya* or *Plectonema* is the correct taxonomic designation of the bloom-forming alga (R.L. Lowe, unpublished data). Published records for *L. wollei* and *P. wollei* from Lake Erie date back to 1898 and 1938, respectively (Pieters 1902, Taft 1942). However, recent increase in soluble reactive phosphorus in western Lake Erie may be an underlying cause of nuisance blooms and shoreline fouling caused by drifting algal mats.

Finally, future environmental change in Lake Erie is anticipated in response to an increasing human population in the watershed, associated changes in land use, and climate change (Lehman 2002, Wolter and others 2006). Clearly, benthic algae provide valuable tools for monitoring changing conditions in the lake. This summary of past algal-based research and outcomes should facilitate design and interpretation of studies and results that detect and explain environmental changes and their causes.

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